

Research Article

Artemia franciscana invasion causes rapid and dramatic ecological changes in hypersaline ecosystems

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Abstract

Aquatic ecosystems are characterised by strong trophic links, which can be profoundly altered by the loss or introduction of species. Invasive species that displace key native species may indirectly affect entire communities and ecosystem functioning. Introduced species often show distinctive traits that facilitate their success, such as reduced susceptibility to parasites that commonly infect native hosts. Here, we examine the ecological consequences of the invasion of the American brine shrimp *Artemia franciscana* on the native clonal species *Artemia parthenogenetica* and their cestode parasites in a hypersaline ecosystem. We carried out monthly sampling (January–June) in Odiel salt pans to compare *Artemia* population structure and cestode infections before (2011) and immediately after (2016) the invasion, quantifying host density, biomass and parasitological status. *A. franciscana* dominated and reached significantly higher densities than the native *Artemia* by the end of the spring 2016. Although both hosts shared the same parasite species, infection levels were markedly higher in the native species (47.33% vs. 5.30% prevalence). The cestode *Flamingolepis liguloides* was 18 times more frequent and induced stronger pathological effects (higher rates of castration and red colouration) in native *Artemia*. Invasive hosts showed a higher proportion of dead *F. liguloides* cysticercoids. The shift in dominant *Artemia* species is likely to affect other community members and ecosystem processes, given the keystone role of *Artemia* in hypersaline ecosystems. Our results highlight the importance of changes in host availability and host-parasite dynamics that can cascade through communities and influence entire ecosystems, particularly in the context of biological invasions.

Key words: *Artemia*, cestode parasites, invasive species, salt pans



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Introduction

To properly secure ecosystem stability and predict their changes, it is essential to understand the direct and indirect ecological and evolutionary impact of invasive species (Haubrock et al. 2025). Aquatic ecosystems are characterised by strong trophic links, which can be profoundly altered by the loss or introduction of species, as these effects can propagate to the entire food web (Gallardo et al. 2016). Particularly understudied

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are the consequences of the invasion through parasite-mediated effects (Hatcher et al. 2015). Parasites play a key role in ecosystems (Lafferty et al. 2008), via density-mediated effects (through mortality) and trait-mediated effects (changes in host phenotype). ‘Cryptic virulence’ – when parasites have low impact on survival – is increasingly acknowledged in ecology, including its role in biological invasions (Hatcher et al. 2014).

Parasites may directly affect host reproduction and survival, which can lower the abundance of host populations (Scott and Dobson 1989; Watson 2013). These density-mediated effects of parasites may indirectly affect other community members which interact with the host species in some way (Dunn et al. 2012). Moreover, the invasive species can also affect the ecosystem functioning via the loss or alteration of ecological and evolutionary processes that parasites can cause through trait-mediated effects, for example, competition, intraguild predation, energy and nutrient flow through the ecosystem (Dunn et al. 2012; Hatcher et al. 2015). While direct density mediated effects have been well studied in the context of biological invasions, the trait-mediated effects are more complex and difficult to reveal and remain largely understudied. In this context, manipulative parasites are of special interest due to their potential to alter a broad range of phenotypic traits in their hosts (behaviour, colour, morphology, physiology) to increase their transmission success (Thomas et al. 2010; Fayard et al. 2020). From an ecological point of view, parasitically modified hosts can be considered as new organisms, entailing new interactions and links with other community members (Lefèvre et al. 2009). From an evolutionary perspective, they are an example of the extended phenotype *sensu* Dawkins (1982).

The crustacean *Artemia* spp. (Branchiopoda, Anostraca) is a keystone and dominant macrozooplankton organism in hypersaline ecosystems. *Artemia* filter-feeds on phytoplankton, affecting their density and consequently water clarity (Mohebbi 2010; Sánchez et al. 2016). At the same time, *Artemia* represents the main prey for numerous water-bird species (Sánchez et al. 2007b; Varo et al. 2011; Lei et al. 2025). Moreover, *Artemia* has an important ecological role as an intermediate host for avian parasites (Sánchez et al. 2013a; Redón et al. 2024). It hosts at least 22 cestode species, each of which infects a specific group of water-birds (flamingos, gulls, shorebirds, grebes or ducks; Redón et al. (2020)) as definitive hosts. These trophically transmitted cestodes induce phenotypic changes in the *Artemia* intermediate host including reversion of phototaxy (from photophobic to photophilic), increased surface and swarming behaviour, changes in colour (from pale pink to bright red via carotenoids accumulation), physiological changes (e.g. accumulation of triglycerides) and gigantism through parasitic castration (by re-allocating energy from reproduction to somatic growth) (Sánchez et al. 2007a, 2016; Redón et al. 2011, 2015; Rode et al. 2013). All these effects enhance both profitability and visibility to the definitive host, so increasing predation (Sánchez et al. 2009). In this way, manipulative parasites have the potential to affect the flow of energy through the food web by intensifying the trophic links involved in their direct and indirect interactions and, consequently, affect the trophic dynamics of the ecosystem (Lefèvre et al. 2009).

The North American brine shrimp *Artemia franciscana* is steadily driving to extinction most native *Artemia* populations in Europe (Amat et al. 2007; Horváth et al. 2018). Cestodes infect the alien *Artemia* species to a lower extent with less pathological effects than for native *Artemia parthenogenetica* and *Artemia salina* hosts in Mediterranean salterns (Georgiev et al. 2007; Sánchez et al. 2012; Redón et al. 2015). However, the processes of extinction of native *Artemia* and the consequences for their parasites remain largely unexplored.

Invasion of *A. franciscana* has been typically reported to occur rapidly (Abatzopoulos et al. 2002; Amat et al. 2005), but the process of this replacement has never been reported. The purpose of the present study is to explore the ecological consequences of the invasion of *A. franciscana*, with special emphasis on the effects to the relationships between *Artemia* and their cestode parasites. We follow the invasion process of *A. franciscana* from the very beginning and compare the population densities of native and invasive species under the same ecological conditions in the Odiel saltpans (Huelva), which was formerly one of the last remaining refuges of native, clonal *A. parthenogenetica* in Spain. This site offered a rare opportunity to investigate the replacement process during an *A. franciscana* invasion and the consequences for the *Artemia* parasite community (but see also Redón et al. (2015)).

Materials and methods

Study area

The present study was carried out in Odiel saltpans (Huelva, Spain, 37°15'29"N, 6°58'25"W, Fig. 1). This wetland complex, located in the south-west of the Iberian Peninsula, is a strategic point on the East Atlantic flyway (Delany et al. 2009) and a regular breeding site for the greater flamingo and its importance for water-birds has led to their protection by national and international laws. The Odiel Marshes are protected as a Biosphere Reserve, a Ramsar site, EU-SPA and a Nature Reserve. The Odiel Marshes have a Mediterranean climate and a typical saltern structure consisting of several ponds through which water circulates, progressively decreasing depth and increasing salinity. Mean monthly temperatures for Huelva, Ronda Este meteorological station went from 11 °C (January) to 22.8 °C (June) in the period 1984–2010 according to the Spanish National Meteorological Agency. The water from the sea is diverted into a complex of large, deep and low-salinity ponds used as water reservoirs (primary evaporation ponds). From these ponds, water passes to a system of larger, shallow and intermediate-salinity ponds, with low invertebrate diversity, highly dominated by *Artemia* (secondary evaporation ponds). Finally, the water is introduced into a series of shallow, roughly rectangular and hypersaline ponds where the salt precipitates and is harvested (crystallisation ponds, see Sánchez et al. (2006b, 2006c)). We conducted our study in the secondary evaporation ponds (Fig. 1) due to their moderate salinity (80–210 g/l) that allows high productivity of *Artemia*, with shallow waters making them accessible to foraging birds (important for efficient parasite transmission). In each pond, we measured water salinity (g/l) with a refractometer and depth (cm). *Artemia* sampling was conducted under permission provided by Junta de Andalucía (1059 Authorisation DGGMN).

Long-term monitoring of *Artemia* in Odiel saltpans

The population dynamics of *Artemia* and their cestode parasites have been monitored regularly since 2000 through a series of complementary research projects and the Odiel saltpans were considered to be one of the last refuges for native *A. parthenogenetica* in the Iberian Peninsula (Pais-Costa et al. 2019, 2021). The last sampling where *A. parthenogenetica* was reported as the sole *Artemia* species was in October 2015 when more than 4.000 individuals were checked from the entire evaporation zone (Sánchez MI, unpublished data). The exotic *A. franciscana* was detected for the first time in January 2016.

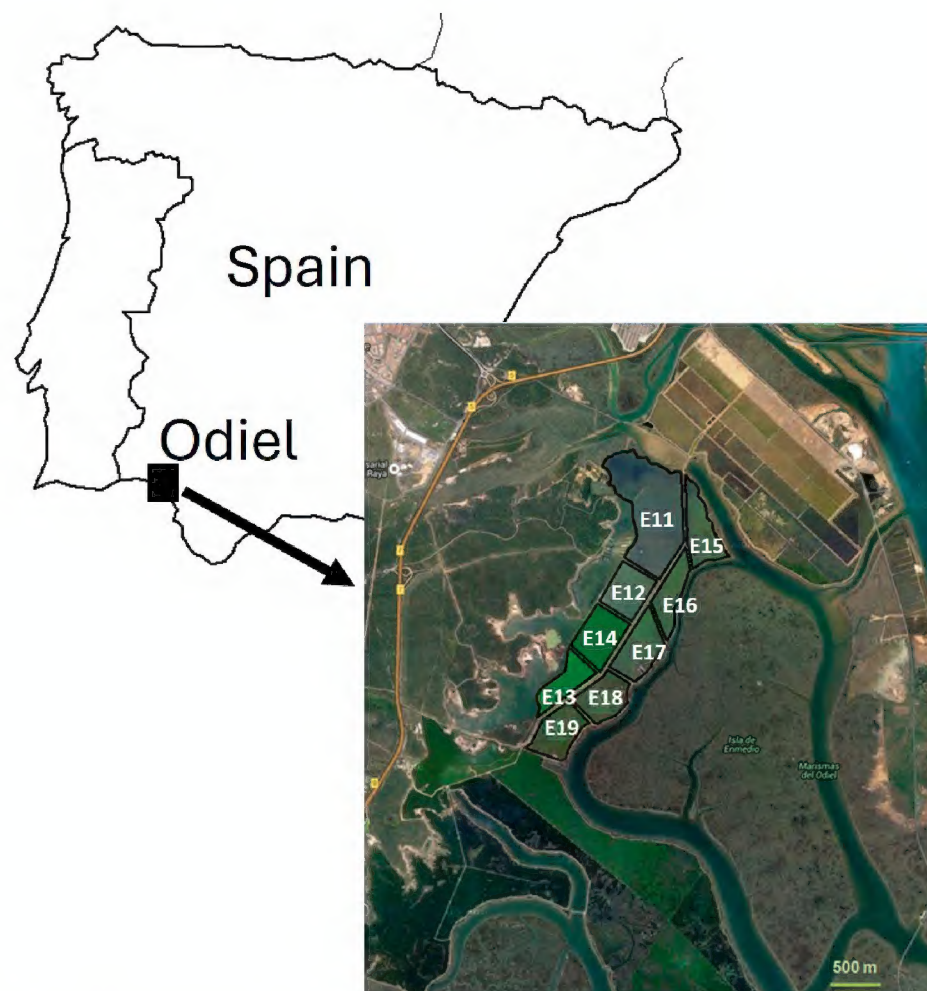


Figure 1. Locations of the studied salt pans in Odiel (Huelva; south-western Spain) containing *Artemia parthenogenetica* and *Artemia franciscana*.

Although the exact monitoring frequency varied amongst projects, sampling was carried out on a regular basis, ranging from bimonthly to semi-annual surveys depending on project objectives. Data collection consistently included estimates of cestode prevalence, abundance and intensity of infection in *Artemia* populations and the density of parthenogenetic *Artemia* (Georgiev et al. 2005, 2007; Sánchez et al. 2006a, 2006b, 2007a, 2013b, 2016). From 2016, several sampling events have been conducted annually to check for the presence of *A. parthenogenetica*. In most surveys, five evaporation ponds were sampled. This monitoring effort provides a robust temporal framework that strengthens the reconstruction of the invasion timeline.

***Artemia* sampling in 2011 and 2016**

We collected monthly *Artemia* samples from January to June in 2011 in one pond (E18) and, in 2016, in nine ponds (Fig. 1), using a 100 µm mesh net. The specimens were transported alive in plastic containers to the laboratory. We collected three different kinds of *Artemia* samples to estimate *Artemia* biomass and density (January to June in 2016, following the procedure described in Sánchez et al. (2006b)) and infection status (January to June in 2011 and 2016, following Georgiev et al. (2005)).

***Artemia* biomass**

To estimate the biomass of *Artemia* in the salt pans, we collected animals from the surface (up to 5 cm depth) and the bottom of the water column (5 cm above the bottom), for 1 minute. Collections were always by the same person to minimise the error associated with different sampling efforts. In the laboratory, samples were washed and placed in an oven at 45 °C for 24 h. Dried samples were then weighed to estimate *Artemia* biomass.

Artemia density

In each pond, a total of 20 litres of water was collected from the central area of the pond to determine the *Artemia* density. This volume represented a composite sample obtained by integrating 20 subsamples of 1 litre collected across the entire water column, which had an average depth of approximately 30 cm. Thus, water samples were not taken at discrete depths, but rather integrated across the full water column of the pond. In the laboratory, we counted the number of adults and juveniles of *A. franciscana* and *A. parthenogenetica* and nauplii of *Artemia* spp. (which cannot be identified to species morphologically).

Cestode infection

In each pond, we collected two *Artemia* samples, one from the surface (up to 5 cm depth) and one from just above the bottom of the water column (5 cm above the bottom), to obtain a minimum of 100 individuals per depth category. In the laboratory, we randomly selected 100 adult *Artemia* per pond and depth of the water column (when *Artemia* were present in the sample) and estimated the proportion of *A. parthenogenetica* and *A. franciscana*. Each specimen was mounted in glycerol and examined under a compound microscope for the presence of parasites. Morphological identification of cestode cysticercoids (the larval stage) was done following Georgiev et al. (2005) and Vasileva et al. (2009). Identification of *Artemia* species was performed following Amat (1985) and Hontoria and Amat (1992). For *Flamingolepis liguloides*, the most prevalent parasite species in adult *Artemia*, we recorded the effect of its associated infection by measuring colour intensity (pale pink vs. bright red), presence or absence of conspicuous lipid granules and reproductive status (castrated vs. reproductive). Castration was assessed, based on female reproductive condition, following standard morphological criteria: adult females with an empty ovisac and no signs of functional ovaries were classified as castrated, whereas females with embryos, nauplii or cysts filling the ovisac or showing evidence of ovulation (oocytes moving along the ovaries or filling the oviducts), were classified as ovigerous. Castration was not assessed in males as it would require detailed spermatogenic analyses of the sexual organs, which requires specialised histological or ultrastructural techniques beyond the scope of this study. We also registered the number of dead and degraded cysticercoids as indicative of an immune response of hosts to infection (see Georgiev et al. (2014); Redón et al. (2015)).

Prevalence (P: proportion of individuals infected), mean abundance (MA: number of parasites averaged for all brine shrimp individuals) and mean intensity (MI: number of parasites averaged for all infected brine shrimp individuals) for each cestode species and for all parasite species together were calculated following Bush et al. (1997). In addition, these indices were calculated independently for *A. parthenogenetica* and *A. franciscana* and for both *Artemia* together.

In 2011, we sampled one of the Odiel ponds used in the present study (E18) as part of a larger scale sampling, during the same period (January-June), following the same protocol. In this way, we were able to calculate infection indices in 2011 and compare them with data from 2016.

Statistical analysis

We used Chi-square tests to compare the relative frequency of *A. parthenogenetica* and *A. franciscana* in the surface and the bottom of the water column for each sampling month in Odiel. We used t-tests or Mann-Whitney U tests to compare *Artemia* biomass between the surface and the bottom of the water column for each month. Generalised linear models (GLM) on *Artemia* biomass (log (biomass + 0.0001) transformed), with normal error and identity-link function, were conducted to test the effect of date and salinity, including the interaction date*salinity. Differences in density between *A. parthenogenetica* and *A. franciscana* from Odiel in a given sample were tested with Wilcoxon Signed Rank tests.

For parasitological analysis, we used Wilcoxon Signed Rank tests (paired data) to compare infection parameters between *A. parthenogenetica* and *A. franciscana* in 2016; and between *A. parthenogenetica* populations in 2011 (when only *Artemia parthenogenetica* was present) and in 2016 (beginning of the invasion process). We compared the vertical distribution of *F. liguloides* (as the most prevalent cestode species) using Chi-square tests. Differences in the frequency of phenotypic changes associated with the infection (castration, colour, lipid granules) between native *A. parthenogenetica* and invasive *A. franciscana* from Odiel 2016, as well as differences in the frequency of dead *F. liguloides* cysticercoids, were assessed with Z tests.

Multiple comparisons were corrected using the False Discovery Rate (FDR) correction. When effects were statistically significant, post hoc LSD tests were applied at a level of $P < 0.05$. Statistical analyses were conducted using STATISTICA software (version 12 StatSoft, Tulsa).

Results

Vertical distribution, density and biomass of *Artemia* during the invasion

To explore the vertical distribution of *Artemia*, a total of 972 *A. parthenogenetica* and 4,659 *A. franciscana* were analysed from the “Cestode infection” sampling. We selected 100 individuals from the bottom and 100 individuals from the surface for each sampling point (see Materials and Methods section). The relative frequency of *A. parthenogenetica* and *A. franciscana* was different in both surface and bottom of the water column (Chi Square test, $P < 0.01$ after FDR correction for all the months; Fig. 2). *Artemia franciscana* was dominant at both water levels, surface ($71.42\% \pm 14.97$, mean $\pm$ SE for the six months) and bottom ($84.10\% \pm 4.51$) (Fig. 2).

Artemia biomass increased from January to June. Higher *Artemia* biomass values were detected in the bottom of the water column along the entire study period, with statistically significant differences in warmer months, from the end of the winter until early summer (4 out of 6 months; Fig. 3A).

The density of *A. franciscana* (AF; 111.36 ± 46.72 , mean $\pm$ SE) was significantly higher than that of *A. parthenogenetica* (AP; 25.77 ± 3.84 , mean $\pm$ SE) in Odiel (Wilcoxon sign-rank test, $P < 0.001$, for 45 paired samples; Fig. 3B). GLM analysis on percentage *A. franciscana* density showed significant effects of date and date*salinity (Suppl. material 1: tables S1, S2). Both *Artemia* species were generally at higher density in warmer months, even though in *A. parthenogenetica* this was only notable in June and in *A. franciscana* from April to June.

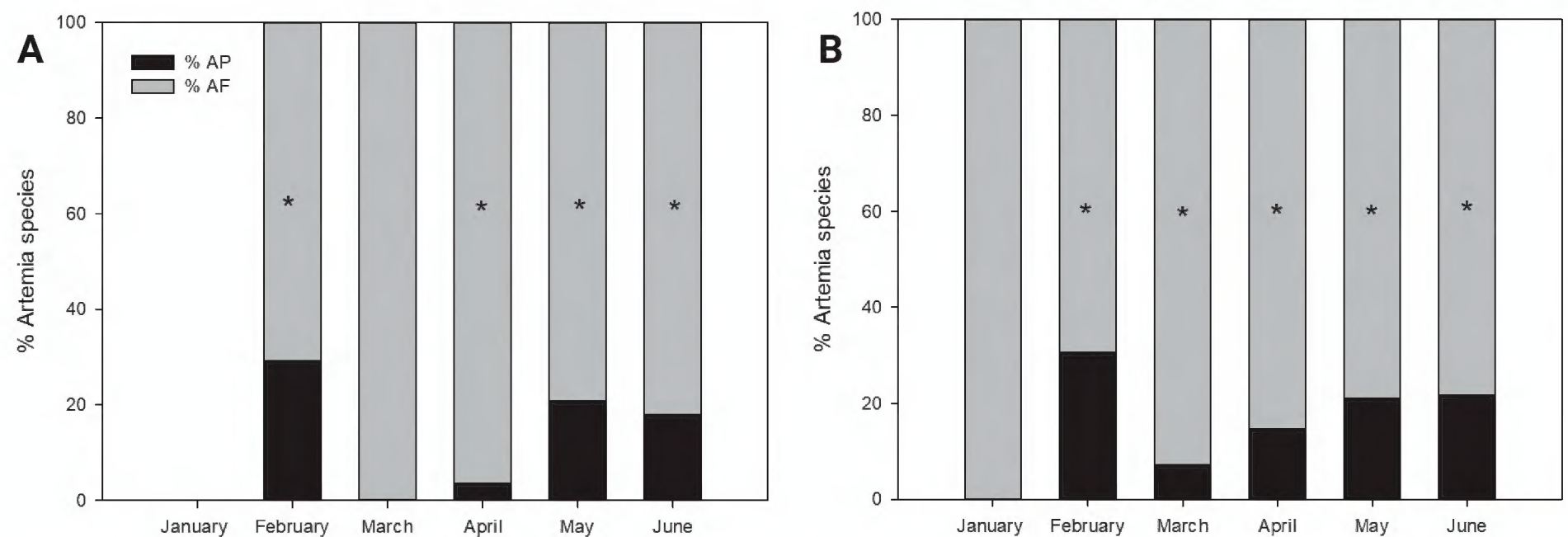


Figure 2. Vertical distribution of *Artemia* species co-existing in Odiel. Percentage of *A. parthenogenetica* (AP; black bars) and *A. franciscana* (AF; grey bars) at the surface (A) and the bottom (B) of the water column, from January to June 2016 in Odiel. *P < 0.01 (Chi-square test, df = 1, after False Discovery Rate (FDR) correction). No *Artemia* were found at the surface in January.

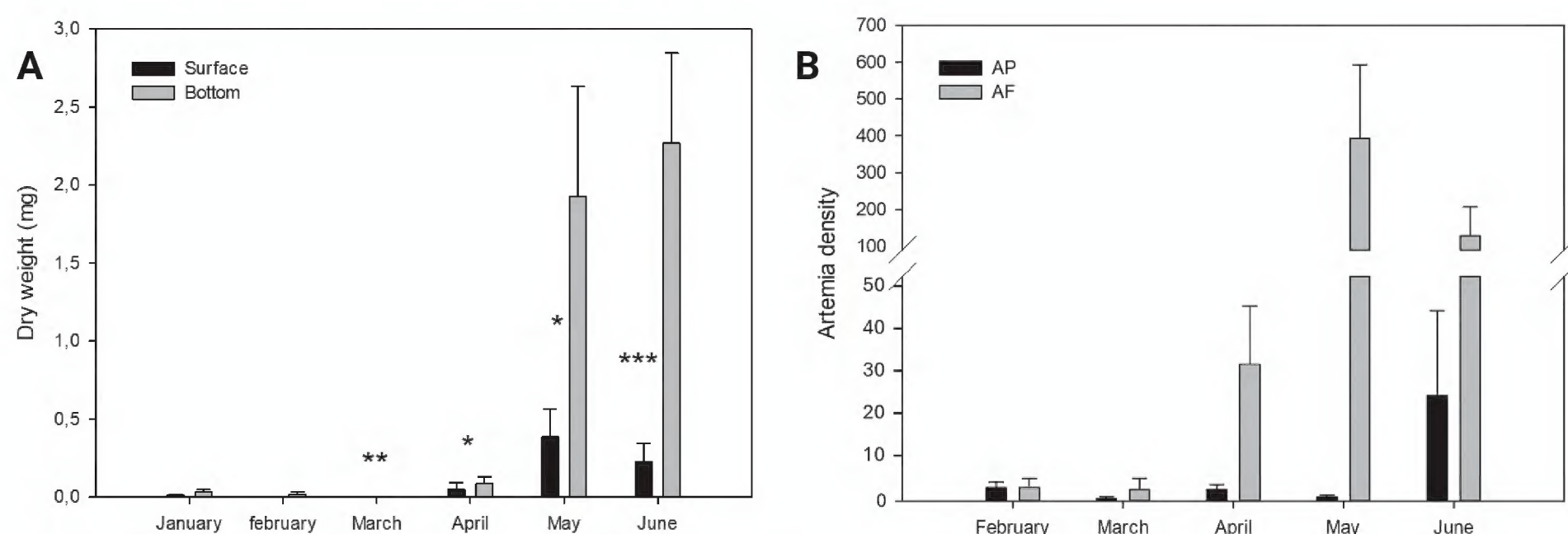


Figure 3. A. Biomass of *Artemia* (mean $\pm$ SE) in the bottom and the surface of the water column in Odiel expressed as dry weight (per unit effort, mg/minute) from January to June 2016. *P < 0.05, **P < 0.01, ***P < 0.001 (t-test or Mann-Whitney U test, df = 5, after FDR correction); **B.** Density of *A. parthenogenetica* (AP) and *A. franciscana* (AF) in Odiel from February to June 2016. No *Artemia* were found at the surface in January.

Cestode parasites in native and introduced *Artemia*

Between January and June 2011, 1,310 *A. parthenogenetica* specimens were examined for cestode parasites. Between January and June 2016, a total of 5,631 brine shrimps from Odiel were analysed for cestodes, including 972 *A. parthenogenetica* and 4,659 *A. franciscana*. Eight cestode species were registered in 2011 and seven in 2016 (when *Wardium stellorae* was absent; Suppl. material 1: tables S3, S4). Prevalence of total cestode infection was 10% higher in 2016 than in 2011 (Suppl. material 1: table S4). The high values of cestode prevalence in both years were mainly due to *F. liguloides* (Fig. 4) that infected 50.00% of parasitised *Artemia* in 2016 and 30.77% in 2011 (Suppl. material 1: table S4). However, the prevalence of all other parasite species was higher in 2011, even though none of these values was significantly different (with *W. stellorae* being absent in 2016 in all the ponds through the study period, Suppl. material 1: tables S4–S6).

In 2016, *A. parthenogenetica* and *A. franciscana* both hosted the same seven species of parasites (Suppl. material 1: tables S5, S6). Overall, 47.33% of *A. parthenogenetica*

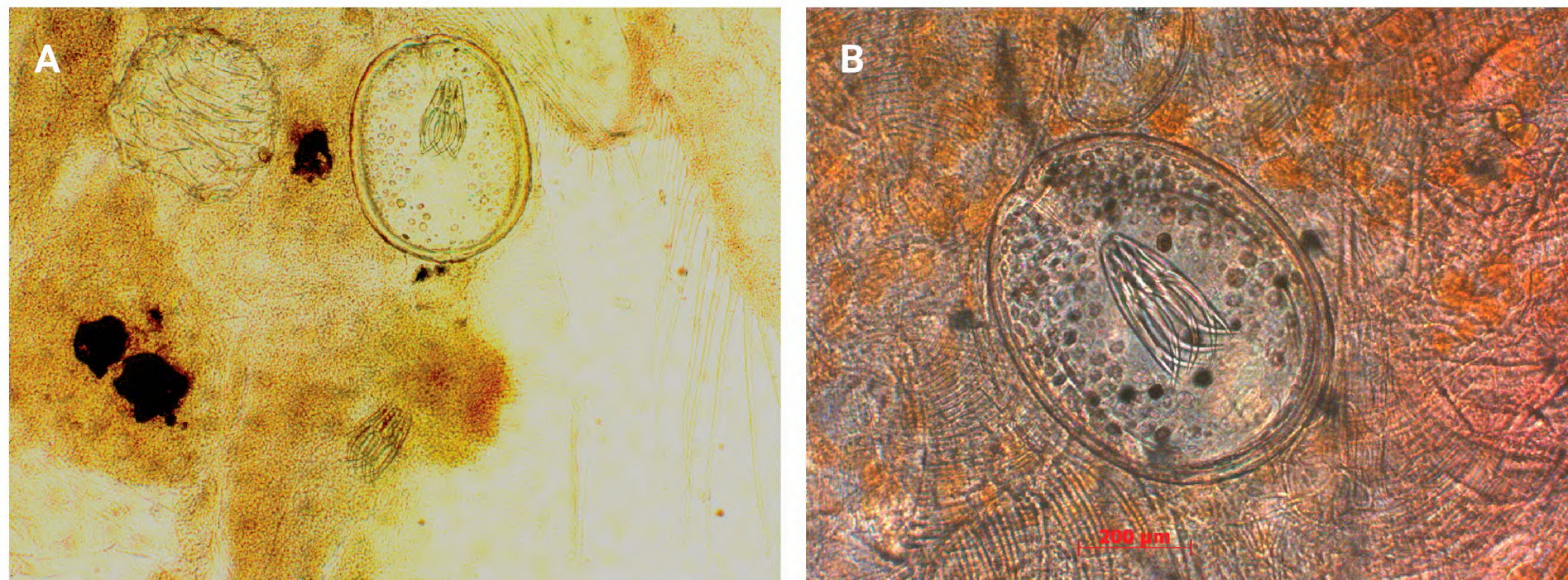


Figure 4. Cystercoids of *Flamingolepis liguloides* in *Artemia* hosts. **A.** On the top left, a dead cystercoid visible as an empty cyst and the hooks outside the cysts at the bottom centre of the image; and on the top centre is a live cystercoid of *F. liguloides* in invasive *A. franciscana*; **B.** Cystercoid of *F. liguloides* infecting native *Artemia parthenogenetica*.

were infected with cestodes (892 cystercoids), but only 5.30% of *A. franciscana* (323 cystercoids) (Table 1). When infected, *A. parthenogenetica* carried up to seven cystercoids per host (reached in May), including different species (i.e. multiple infections). Similar values were detected for *A. franciscana*, with a maximum of eight cystercoids per individual.

P%, MA and MI for total cestode infection were significantly higher in *A. parthenogenetica* than in *A. franciscana* (Table 1). Amongst the seven parasite species registered in 2016, significantly higher prevalence was detected in *A. parthenogenetica* than in *A. franciscana* for four of them (Table 1). *F. liguloides* (parasite of flamingos) was the most common parasite, but prevalence values differed greatly between host species. *A. parthenogenetica* was 18 times more likely to be infected by this cestode species compared to *A. franciscana* (Table 1, Suppl. material 1: tables S5, S6).

Considering all *F. liguloides*-infected specimens during the study period, 96.5% of *A. parthenogenetica* females were castrated, compared with 64.5% *A. franciscana* females ($Z = 9.689$, $P < 0.001$). All non-infected *Artemia* adult females were reproductive individuals. The proportion of *F. liguloides*-infected *A. parthenogenetica* that were bright red was significantly higher than in infected *A. franciscana* (55.6% of *A. parthenogenetica* vs. 18.7% of *A. franciscana*; $Z = 6.743$, $P < 0.001$). However, the presence of lipid granules did not differ between the two *Artemia* species (13.1% in *A. parthenogenetica* vs. 10.3% in *A. franciscana*; $Z = 0.621$, $P = 0.534$). In addition, while only 0.3% of the total *F. liguloides* cystercoids ($n = 804$) registered in *A. parthenogenetica* were dead, this value reached 13.3% ($n = 158$ cystercoids) in the case of *A. franciscana* ($Z = 9.239$, $P < 0.001$, Fig. 4).

Prevalence of infected individuals was similar between the surface and the bottom of the water column (Wilcoxon signed Rank test, $P > 0.115$ for the three populations). Comparisons of *F. liguloides* prevalence between the bottom and surface of the water column in June (when this parasite species was more prevalent) did not show significant differences for *A. parthenogenetica* (Chi squared test, $P > 0.110$), except for one pond (E18) where prevalence was significantly higher at the bottom (Fig. 5A). In general, the values were higher at the bottom compared with the surface. *A. franciscana* showed a similar distribution of infected individuals between the surface and the bottom of the water column ($P > 0.126$; Fig. 5B).

Table 1. Comparison of total prevalence (P%), mean abundance (MA ± SE) and mean intensity (MI ± SE) of cestode parasites between *A. parthenogenetica* and *A. franciscana* from Odiel (SW Spain), January to June 2016. Paired t-test or Wilcoxon signed rank tests were used to compare infection rates between months. Significantly higher values are shown in bold.

Cestode species	Infection descriptors	<i>A. parthenogenetica</i> n = 972	<i>A. franciscana</i> n = 4,659	Z	p-value	U	p-value
Fam. Hymenolepididae							
<i>Flamingolepis liguloides</i>	P%	44.14	2.43	40.05	< 0.001		
	MI	1.87 ± 1.05	1.40 ± 0.09			17281	0.0000001
	MA	0.83 ± 0.04	0.034 ± 0.004			1312879	0.001
<i>Flamingolepis flamingo</i>	P%	2.57	0.60	5.61	< 0.001		
	MI	1.08 ± 0.06	1.11 ± 0.11			335.5	0.53336
	MA	0.03 ± 0.01	0.01 ± 0.01			2219630	0.0000001
<i>Confluaria podicipina</i>	P%	0.21	0.30	0.17	0.86		
	MI	1.00 ± 0.00	1.14 ± 0.10			12	0.67817
	MA	0.002 ± 0.001	0.003 ± 0.001			2262127	0.613552
<i>Wardium stellorae</i>	P%	0.00	0.00	–	–		
	MI	0.00	0.00			–	–
	MA	0.00	0.00			–	–
<i>Fimbriarioides tadornae</i>	P%	0.21	0.06	0.75	0.45		
	MI	1.00 ± 0.00	1.33 ± 0.33			2	0.68309
	MA	0.002 ± 0.001	0.001 ± 0.001			2261074	0.178547
Fam. Dilepididae							
<i>Eurycestus avoceti</i>	P%	2.37	1.03	3.24	0.001		
	MI	1.04 ± 0.04	1.06 ± 0.05			551.5	1.000
	MA	0.03 ± 0.01	0.01 ± 0.002			2234023	0.000686
<i>Anomotaenia</i> spp.	P%	3.29	1.18	4.71	< 0.001		
	MI	1.00 ± 0.00	1.02 ± 0.02			864	0.45994
	MA	0.03 ± 0.01	0.01 ± 0.002			2216476	0.000001
Fam. Progynotaeniidae							
<i>Gynandrotaenia stammeri</i>	P%	0.10	0.15	-0.11	0.91		
	MI	1.00	1.14 ± 0.14			0	1.000
	MA	0.001 ± 0.001	0.002 ± 0.001			2263201	0.721397
TOTAL	P%	47.33	5.30	35.91	< 0.001		
	MI	1.94 ± 0.05	1.31 ± 0.05			35847	0.0000001
	MA	0.92 ± 0.04	0.07 ± 0.01			1291783	0.001

Discussion

The present study is the first to document the replacement of native *Artemia* by invasive *A. franciscana*, following the invasion process from its earliest stages. Only *A. parthenogenetica* was present in the Odiel marshes in 2014 (Pais-Costa et al. 2021) and in October 2015 (Sánchez MI, unpublished data). After June 2016, no *A. parthenogenetica* were found in Odiel salt pans in any of the following monitoring samplings. The rapid replacement observed here helps explain why native *Artemia* have disappeared so quickly from other sites in the Mediterranean Region once the exotic congener becomes established (Amat et al. 2007; Horváth et al. 2018) and why cases of long-term co-existence are extremely rare. Our results also suggest that

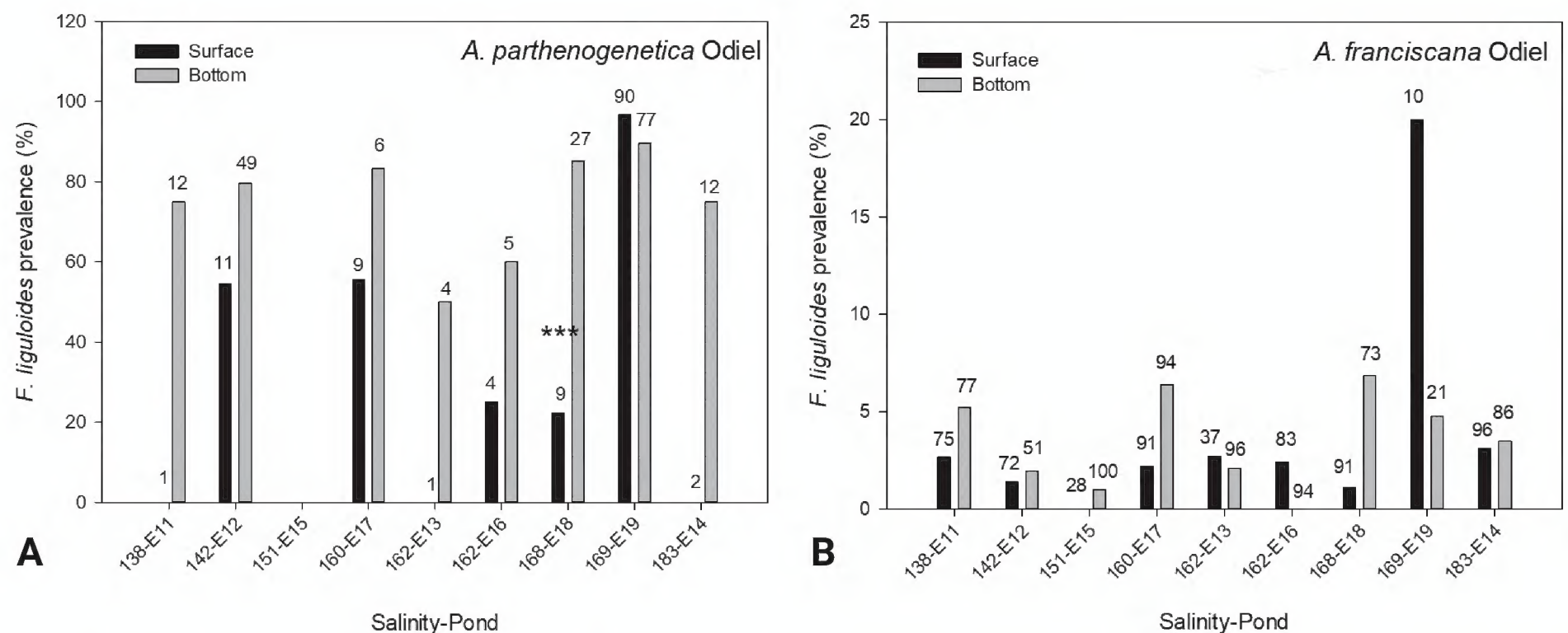


Figure 5. Vertical distribution of infected *Artemia*. Proportion of *Artemia* infected with *Flamingolepis liguloides* at the surface (black bars) and bottom (grey bars) of the water column, in several evaporation ponds in Odiel in June 2016. **A.** *A. parthenogenetica* and **B.** *A. franciscana*. Ponds are listed in order of increasing salinity (g/l) from left to right. Sample sizes are given above the bars. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ after FDR correction.

this fast replacement may be facilitated by the density- and trait-mediated effects of native cestode parasites that predominantly affect native *Artemia*. Consequently, the replacement of native *Artemia* species by the exotic congener is likely to strongly alter host-parasite dynamics in hypersaline systems. Finally, our results raise the possibility of parasite co-extinction resulting from the invasion of a poorly-compatible host that outcompetes the native host species (Dallas and Cornelius 2015).

Consequences of the invasion for native *Artemia* populations

Previous studies indicate that *A. franciscana* can outcompete native *A. parthenogenetica* and *A. salina* within two or three generations under laboratory conditions (Abatzopoulos et al. 2002; Amat et al. 2005). Moreover, *A. franciscana* were found to reach maturity earlier, have shorter generation times and exhibit shorter intervals between broods than *A. parthenogenetica* (Amat et al. 2007; Aubakirova et al. 2024). However, we provide the first evidence from the field, suggesting that such species replacement may occur even faster. It is known that *A. franciscana* is highly thermotolerant (Gbotsyo et al. 2020) and has wider tolerance to temperature compared to *A. parthenogenetica* (Browne and Wanigasekera 2000). This allows the invasive species to colonise the environment during winter, when the native *Artemia* is absent (it overwinters in the form of resistant cysts). At that time, phytoplankton density is high, enabling *A. franciscana* to exploit a temporally empty niche and become established. In spring, when the first annual generation of *A. parthenogenetica* starts hatching, *A. franciscana* may already dominate due to its high reproductive rate and fecundity, high tolerance to low temperatures and lower susceptibility to parasites (Sánchez et al. 2012; Redón et al. 2015). At the same time, native *Artemia* experience higher levels of parasitic castration and increased predation risk by birds due to parasite-induced changes in host behaviour and colouration, as shown in previous studies (Sánchez et al. 2007a, 2009; Redón et al. 2011).

Consequences for the population dynamics of parasites

Our study system provided a valuable opportunity to investigate the infection dynamics in co-evolved vs. non-co-evolved host-parasite interactions. As predicted by the ‘enemy release hypothesis’ (Colautti et al. 2004), *A. franciscana* showed substantially lower infection levels and reduced parasite-induced effects compared to native *Artemia* co-occurring in Odiel. Similar patterns have been shown in the few Spanish and French populations where native and alien congeners co-exist (Sánchez et al. 2012; Redón et al. 2015). These differences are likely explained by the distinct co-evolutionary history between hosts and parasites. The native *Artemia* experienced stronger pathological effects associated with the infection, including changes in colour and castration. These results are consistent with a previous study comparing co-existing *A. franciscana* and the native sexual species *A. salina*, where cestode infection caused red colouration and castration in a high proportion of native hosts, with the exotic species being significantly less affected (Georgiev et al. 2014; Redón et al. 2015).

On the other hand, we found evidence suggesting a stronger immune response in *A. franciscana* as indicated by the higher proportion of degraded cysts, compared with *A. parthenogenetica*. This likely reflects the short evolutionary association between the invasive host and native parasites. Similar patterns have been reported in other host-parasite systems, such as the invasive round goby (*Neogobius melanostomus*), in which the acanthocephalan parasite *Neoechinorhynchus tenellus* showed reduced survival compared with infections in native fish hosts (Gendron and Marcogliese 2016). Cystacanths died prematurely in the novel host, while parasites were intact in two co-occurring native hosts, johnny darters (*Etheostoma nigrum*) and logperch (*Percina caprodes*).

Given that *Artemia* becomes infected by accidentally ingesting cestode eggs released into the water with bird faeces (Georgiev et al. 2005), a significant fraction of the available cestodes may enter the invasive *A. franciscana*, where many fail to develop successfully, resulting in a net loss of parasites from the system. This process could potentially generate a dilution effect (Telfer et al. 2005; Kopp and Jokela 2007; Lettoof et al. 2013) reducing parasite transmission to suitable native hosts (Johnson and Thielges 2010; Lettoof et al. 2013). However, contrary to this expectation, native *Artemia* did not experience a decrease in infection levels following the invasion. Instead, infection indices were generally higher in 2016 compared with 2011. This high parasite pressure on native populations (more than 80% of the *A. parthenogenetica* individuals were infected by the castrating cestode *F. liguloides* in June) may have contributed to the rapid replacement of native *Artemia* by the invasive congener.

Over longer time scales, interactions between the exotic hosts and native parasites may change through evolutionary processes (Decaestecker et al. 2007). Alternatively, the decline or extinction of native *Artemia* could lead to co-extinction of their specialised cestode parasites, if infection levels fall below the threshold required for parasite persistence (Deredec and Courchamp 2003).

Consequences of parasite loss for the functioning of hypersaline ecosystems

The low susceptibility of the invasive *Artemia* to native parasites may have a wide range of direct and indirect ecological and evolutionary consequences. In particular, it may alter consumer–resource interactions across multiple trophic levels. For example, parasites are known to decrease feeding rates in native *Artemia* (Sánchez

et al. 2016) and the low effect of parasites on the invasive *Artemia* may lead to higher grazing pressure on phytoplankton density and potentially trigger cascading effects (Anaya-Rojas et al. 2019). On the other hand, trophically transmitted parasites can improve the trophic value of ecosystems by facilitating prey consumption by birds (Lefèvre et al. 2009). Prey selection experiments show that shorebirds preferentially feed on infected red *Artemia*, which are more visible, accessible and profitable from an energetic point of view (Sánchez et al. 2009). Therefore, water-birds may have lower foraging intake rates when feeding in salt ponds invaded by *A. franciscana*. Given the abundance of *Artemia* and the importance of infected individuals for birds, the loss of parasites may alter the food web properties, as well as energy and mass flow in hypersaline ecosystems.

Conclusions

The invasive *Artemia franciscana* outcompeted native congeners at high velocity, simultaneously disrupting the transmission of avian cestode parasites. Native *A. parthenogenetica* act as a highly suitable intermediate host for several avian cestodes, supporting successful parasite development. In contrast, *A. franciscana* is highly resistant to infection by many of these cestode species, resulting in reduced prevalence and intensity of infection. Consequently, the rapid dominance of *A. franciscana* leads to a marked decline in parasite transmission. These changes have implications beyond host population dynamics, as parasites constitute a substantial and often overlooked component of biodiversity. More research integrating different aspects of the biology and ecology of hosts and parasites is necessary to better understand biological invasions in hypersaline ecosystems and predict associated impacts.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.

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Author contributions

DL: Formal analysis, Writing – Original draft, Writing – Review and Editing; SR: Formal analysis, Writing – Original draft, Writing – Review and Editing; MM: Investigation, Writing – Original draft; FH: Investigation, Writing – Review and Editing; AJG: Conceptualization, Methodology, Formal analysis, Resources, Writing – Review and Editing, Visualization, Project administration, Funding Acquisition; MIS: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data Curation, Writing – Original draft, Writing – Review and Editing, Visualization, Supervision, Project administration, Funding Acquisition.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Supplementary tables

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